

Natural history observations on *Bitis peringueyi* (Boulenger) (Reptilia: Viperidae)

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We report reproductive data from five clutches of Peringuey's Adder, *Bitis peringueyi* (Boulenger), from females recently collected near Swakopmund, Namibia. Litter sizes ranged from two to seven with relative clutch masses (litter mass divided by post-parturient maternal mass) of 0.15-0.92. Tail colour dimorphism of the females and the offspring support previous contentions of a non-sex-linked two allele system with tan dominant to black. Our data suggest, however, that the dominant allele (tan) has a relatively low frequency in the population.

INTRODUCTION

Natural history and reproductive biology are inadequately known for most of the African vipers in the genus *Bitis* Gray, 1842, and much is yet to be done before we can understand patterns of life history variation in this interesting group of snakes. This genus alone encompasses all of the litter size variation in snakes having both the largest known litter and among the smallest (Spawls & Branch 1995). Understanding the evolutionary processes that gave rise to such diversity will require quantitative reproductive data placed in a historical framework. Detailed studies of reproductive biology (e.g., Luiselli *et al.* 1998; Shine *et al.* 1998) will contribute most to future evolutionary research, but smaller contributions can significantly speed the process of discovery. Precise information, with sample numbers and calculated averages, about relative clutch mass, reproductive interval, and age/size at maturity are lacking for most species of *Bitis*.

Peringuey's Adder, *Bitis peringueyi* (Boulenger, 1888), is endemic to the Namib Desert of southwestern Africa (e.g., Broadley 1983, Spawls & Branch 1995). It is one of the smallest members of the genus and is the most specialised for life

in shifting dune sand (Broadley 1983). *Bitis peringueyi* use sidewinding locomotion, readily bury into sand, and have eyes and nostrils situated dorsally to allow nearly complete submersion in sand without impeding vision or respiration. The main prey of this species are diurnal lacertids and nocturnal geckos (Branch, 1978). Robinson & Hughes (1978) presented size data and number of young from four female *B. peringueyi*, as well as information on tail colour dimorphism. Herein we provide data for five additional litters of *B. peringueyi*, report further on tail colour variation, and present the first information on relative clutch mass for this species.

METHODS

On 26 March 1998, one adult male, seven adult females, and one neonatal male *Bitis peringueyi* were collected 6.0-8.8km south of the Swakop River along the B2 highway, Erongo Region, Namibia. Animals were collected on the flat desert at the western edge of dune slopes. Collection occurred from 1000-1500 under a high fog with an air temperature of 20°C. All but one animal was collected from the fine sand skirt around isolated *Zygophyllum stapffii* Shinz (Zygophyllaceae), the dominant plant in the area

(D. DeNardo, pers. obs.). Animals were either completely exposed, completely submerged under the sand, or predominantly submerged with the dorsal surface of their head exposed. Most animals had fresh tracks associated with their position, suggesting relatively recent movement to that position. The adult male was found under an old tire. Snakes were sexed by manually expressing the cloaca to expose either hemipenes

Table 1. Body size and reproductive values for five female *Bitis peringueyi*. Relative clutch mass (RCM) and relative burden (RB) is calculated from individual statistics. The asterisk (*) indicates an adjusted value (*vide* Methods).

Female #:	2	3	6	7	8
SVL (mm)	260	268	284	254	305
Post-partum mass (g)	14.09	24.67	19.65	12.20	29.45
Total litter mass (g)	9.30	3.58	13.96*	11.50	14.89
RCM	0.66	0.15	0.71	0.92	0.51

Five of the females were pregnant when captured. On 3 April, the morning prior to shipping, one female gave birth to a full litter of five young, while a second female gave birth to three young. This second female gave birth to four additional young on 13 April, after arriving at UCB. The remaining three females produced young after arriving at UCB. We processed all snakes initially on 8 April, and thereafter we re-processed individual females and took initial data on their litters on the day following birth of young. For each specimen the following data were taken: sex, mass, snout-vent length (SVL), tail length (TL), and tail colour. Relative clutch mass (RCM) was calculated for all reproductive females. RCM was defined as litter mass divided by post-parturient maternal mass (Shine 1980). We provide values necessary for alternate RCM calculations (e.g., Seigel & Fitch 1984). To provide the RCM value for one female (number 6), we had to estimate the mass of one neonate that died of accidental trauma several hours before processing and had begun to desiccate. A regression analysis of SVL and mass of its siblings showed a tight correlation ($r^2 = 0.96$) with values bracketing the estimated mass (= 2.16 g, measured mass = 1.33 g). Additionally, female number 7 gave birth to three young in Africa

or oviductal papillae. On 3 April, animals were exported to the University of California, Berkeley (UCB), California, USA and maintained in 40 litre aquaria. Aquaria were set up with loose sand and sub-surface heating at one end of the cage to provide a thermogradient. Room temperature was 22°C with a photoperiod of 12L:12D. Animals were fed small lizards or neonatal mice.

before measurements were taken. These young were transported in deli cups containing well moistened sand, so fluid loss should have been minimal, but, to be sure, we performed a regression analysis of mass and SVL of all neonates except the desiccated one ($r^2 = 0.86$, $n = 26$). In the latter regression, 6% of the variance was explained by a single individual from female number 7, but this neonate was born following shipment, and was processed promptly. It is possible that error was introduced during measurement of this individual. Regressions were used only to reduce or identify potential error, not to test significance, and the adjustment made for one neonate does not greatly effect our conclusions.

RESULTS

Reproductive data for the five pregnant females are presented in Table 1. Data for each litter are provided in Table 2. Tail colour varied within and among litters (Table 2), some litters being dimorphic, while others showed only the black colour variant. For one litter, the time of birth was known because births took place just prior to or during the initial processing of females and young. These neonates were alert and active af-

ter emerging from the sand. The activity of the young began to subside a few hours after birth. Some young did not complete tail rubbing without manual assistance. Face rubbing was not included face rubbing.

Table 2. Data for five litters.

Young of female
Birth date
Number in litter
Mean SVL (mm) \pm 1 SD
(Range)
Mean mass (g) \pm 1 SD
(Range)
Sex ratio (σ : ρ)
Tail colour (tan:black)
Mother's tail colour

DISCUSSION

Females did not appear to give birth following shipment (Madsen & Shine 1999). The SVL of all the neonates in this study were within the range reported by Hughes (1978), i.e. 244-325 mm. The 27 young had a SVL within the range reported (116-135 mm) by Hughes (1978), yet the 27 young had a higher mass (1.33 g) than reported (1.0-1.5 g) by Hughes (1978). Whether this is a true difference in lean mass (snakes) or simply water

Mean RCM for all *B. peringueyi* litters, which approximates the RCM calculated from raw data reported by Robinson & Hughes (1978) also near the average calculated for a viviparous terrestrial snake, influenced, however, by the small number 3, a value that is lower than others. We believe this is a relatively small litter for

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ter emerging from their embryonic sacs, and all of the young began to moult from just minutes to a few hours after birth, although some of them did not complete the process and required manual assistance. First post-birth behaviours included face rubbing, mouth gaping, tongue

flicking, defensive hissing and striking, and sidwinding locomotion. Several of the young submerged themselves in the sand substrate within 20 minutes after birth, others moved around the enclosure for an extended time before submerging.

Table 2. Data for five *Bitis peringueyi* litters. Adjusted value is marked by an asterisk (*).

Young of female #:	2	3	6	7	8
Birth date	3 April	15 April	21 April	3,13 April	8 April
Number in litter	5	2	6	7	7
Mean SVL (mm) \pm 1 SD (Range)	108 \pm 3.3 (104-112)	106 \pm 2.8 (104-108)	115 \pm 4.5 (109-119)	105 \pm 8.1 (90-114)	112 \pm 4.5 (110-115)
Mean mass (g) \pm 1 SD (Range)	1.86 \pm 0.11 (1.74-1.98)	1.79 \pm 0.24 (1.62-1.96)	2.32 \pm 0.14* (2.14 - 2.48)	1.64 \pm 0.37 (0.92 - 2.07)	2.13 \pm 0.14 (2.03-2.27)
Sex ratio (σ : ρ)	3:2	1:1	1:5	3:4	4:3
Tail colour (tan:black)	4:1	1:1	0:6	6:1	0:7
Mother's tail colour	tan	tan	black	tan	black

DISCUSSION

Females did not appear to be particularly emaciated following birth, as do some other viperids (Madsen & Shine 1992; Reiserer, unpublished). The SVL of all the adult females were within the range reported by Robinson & Hughes (1978), i.e. 244-325 mm. Four of the litter sizes in this study were within previously reported ranges (3-10, Branch 1988; 4-10, Robinson & Hughes 1978), but herein we report the possible minimum litter size of two. All but one of the 27 young had a SVL shorter than previously reported (116-135 mm, $n = 16$, Robinson & Hughes 1978), yet the vast majority of neonates had a higher mass (1.6-1.7, $n = 4$, Robinson & Hughes 1978). Whether this difference reflects true difference in lean dry mass (e.g., stockier snakes) or simply water content is unknown.

Mean RCM for all *B. peringueyi* litters was 0.59, which approximates the value (0.53) we calculate from raw data reported for a single clutch by Robinson & Hughes (1978). This value is also near the average calculated by Shine (1992) for a viviparous terrestrial snake. This value is influenced, however, by the low RCM of female number 3, a value that contrasts with the others. We believe this female gave birth to an unusually small litter for her body size. Omitting

her RCM from our calculated mean (=0.59), we obtain an RCM of 0.70. Both values are, however, within the normal range for a terrestrial viviparous snake (Shine 1992).

Dimorphism in tail coloration is known in a number of snakes that use the tail to lure for prey (Burger & Smith 1950, Heatwole & Davison 1976, Pycraft 1925, Tryon reported in Strimple 1992). Caudal luring has been reported for *B. peringueyi* (Branch 1988, FitzSimons 1962), as well as for *B. caudalis* (A. Smith, 1838), which also displays tail colour dimorphism (Branch, 1988). Similar dimorphism is known in *B. schneideri* (Boettger, 1886), the more southerly ecological counterpart of *B. peringueyi* (Broadley 1983), but it is unknown whether this species employs luring. Robinson & Hughes (1978) considered the probable genetic basis of tail colour dimorphism in *B. peringueyi*. Their study used a series of 69 snakes (live and preserved, only four of which were related by parentage) to determine a ratio of the two colour morphs (=2.8:1, tan:black), and they concluded that the trait was controlled by a non-sex-linked two allele system with tan dominant to black. Our data are consistent with their conclusion, however, our data suggest that the dominant allele (tan) has a low frequency in the population.

If a two allele, autosomal, simple dominance system exists, we expect to find four types of phenotypic distribution associated with litters: 1) those with all neonates having tan tails, representing the majority of litters because they result from three of the six possible crosses (i.e., one or both parents homozygous dominant); 2) those with all black tails, from homozygous recessive parents; 3) those with about 50% of each morph, from one heterozygous and one homozygous recessive parent; and 4) those with a 3:1 ratio of tan to black tails, the result of two heterozygous parents. Our sample contained no case 1 litters, two probable case 2 litters, and three mixed phenotype litters (small litter sizes prevent discrimination between case 3 and 4). Tail coloration in our females (Table 2) is consistent with and adds support to this interpretation. The lack of a case 1 litter (all neonates with tan tails) means that no parent (male or female) was homozygous dominant. By representing the dominant and recessive alleles as T and t, respectively, and using Mendelian genetics, we determined the frequency of T in our sample to have a probable frequency of 0.26 (range possible = 0.20-0.39). Given 27 offspring and a T frequency of 0.26, we expect 12 tan-tailed and 15 black-tailed young (sample = 11:16). Random error is expected for a sample of this size, and we consider these data to be inconclusive, but suggestive. Future research on the genetic basis of tail dimorphism of wild caught female *B. peringueyi* with litters should concentrate on documentation of the distribution of the trait in mother and young.

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It is a great pleasure to
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